PROC. ENTOMOL. SOC. WASH.
95(4), 1993, pp. 547–553

ON THE BIOLOGY OF *PENEPODIUM GORYANUM* (LEPELETIER) IN WOODEN TRAP-NESTS (HYMENOPTERA, SPHECIDAE)[1]

MARCOS V. B. GARCIA AND JOACHIM ADIS

(MVBG) EMBRAPA—Centro de Pesquisa Agroflorestal da Amazônia, Caixa Postal 319, 69.000 Manaus/AM, Brazil; (JA) Max-Planck Institut für Limnologie, AG Tropenökologie, Postfach 165, D-24302 Plön, Germany.

Abstract.—The nesting habits and life cycle of *Penepodium goryanum* (Lepeletier) 1845 were studied in 1991 in a central Amazonian blackwater inundation-forest. Nests were obtained from artificial sites for nesting (trap-nests) and consisted of a single cell per cavity, provisioned with cockroaches of the genus *Eunyctibora*. The characteristics of the nest are given as well as information on the life cycle, seasonality, parasites and prey preferences of *P. goryanum*. The effects of the flood pulse on the seasonality of *P. goryanum* are discussed.

Resumo.—O hábito de nidificação e biologia de *Penepodium goryanum* (Lepeletier) 1845 foram estudados em uma floresta de inundação (igapó) na Amazônia Central, durante 1991. Ninhos foram obtidos em ninho-armadilhas artificiais e consistiam em única célula por cavidade, provisionada com baratas do gênero *Eunyctibora*. Características do ninho são fornecidas bem como informações sobre o ciclo de vida, sazonalidade, preferência por presas e parasitismo de *P. goryanum*. Os efeitos do pulso de inundação na sazonalidade de *P. goryanum* são discutidos.

Key Words: Nesting habits, inundation, Amazon, Neotropics, Sphecidae

The new genus *Penepodium* Menke was described in Bohart and Menke's (1976) revision of the Sphecidae. They list 22 species and these are distributed from Mexico to Argentina. Biological data exist for only a few species: Williams (1928) described in detail the nesting habits of *P. haematogastrum* (Spinola) and *P. luteipenne* (Fabricius) (as *flavipenne*), and Richards (1937) provided notes on *P. mocsaryi* (Kohl) and *P. goryanum* (Lepeletier).

Scarcity of biological data on solitary wasps is due principally to the difficulty in locating their nests. Using wooden trap-nests (artificial sites for nesting) permits one to collect and study species which use pre-existing holes for nesting. In this paper we present data on the nesting habits and life cycle of *Penepodium goryanum* reared in trap-nests.

STUDY AREA AND METHODS

The study was carried out during 1991. The study area is a blackwater inundation-forest located about 20 kilometers upstream from Manaus on the left bank of the Rio Tarumã-Mirím (03°02′S, 60°11′W), a tributary of the Rio Negro (cf. Adis 1992a). This area is subject to a rainy season (between December and May, with a mean precipitation of ca. 1550 mm), and a "dry" (drier)

[1] From cooperation between Max-Planck-Institute for Limnology, Tropical Ecology Working Group, Plön, Germany, and National Institute for Amazonian Research (INPA), Manaus/AM, Brazil.

season, (between June and November, with a mean precipitation of ca. 550 mm) (cf. Ribeiro and Adis 1984). The inundation forest is covered by several meters of flood water for five to seven months each year (March/April–August/September), depending on the terrain elevation (cf. Adis 1992b).

Various investigators have successfully used the trap-nest method for study of the biology and population dynamics of solitary wasps and bees (cf. Medler 1967, Krombein 1967, Medler and Fye 1956, Matthews and Fischer 1964, Collins and Jennings 1984, Jayasingh and Freeman 1980, Coville and Coville 1980, Fricke 1991).

Different authors have used trap-nests of various dimensions and made out of different materials, according to the objectives of their studies. In our case we adopted trap-nests similar to those used by Medler (1967) and Krombein (1967), but slightly modified. We used blocks of wood (*Protium* sp., Burseraceae) 40 × 40 × 100 mm, drilled longitudinally to a depth of 80 mm with the apertures, 4.8, 9.5 and 12.7 mm in diameter. Before being drilled, the wood blocks were sawed in half longitudinally and then held together with adhesive tape to permit the examination of the cavities when opened. Nine blocks (3 of each diameter) were held together with a rubber band (Fig. 1G). Forty bundles were attached to tree trunks horizontally (two per tree). One bundle was placed at a height of 5 meters (above the maximum flood level) and one at about 2.5 meters, in the inundation stratum of the forest. The latter was moved according to the water-level to prevent flooding. Bundles with traps made out of different wood, *Triplaris surinamensis* Cham. (Polygonaceae), *Macrolobium acaciaefolium* Benth. (Leg., Caesalpiniaceae), *Aldina latifolia* Spruce ex Benth. var. *latifolia* (Leg., Fabaceae) and *Mora paraensis* Ducke (Leg., Caesalpiniaceae) were attached to four trees. Traps were examined approximately every 15 days and those with completed nests were collected and substituted by another of the same diameter.

Results

Characteristics of the nests

The nest consisted of one single cell closed at the entrance with a plug of mud, 3.7–7.4 mm thick (mean = 5.1 ± 1.0, N = 20). The external surface of the closing plug had a coating of resin (N = 29) (Fig. 1H), plant wax (N = 11) or bits of debris such as small pieces of leaves, lichens or fragments of wood adhering to the coating of resin (N = 9). In general the nest was closed only with a single wall (N = 105), but some had two, side by side (N = 2), or separated by a distance of 7.4–14.8 mm (mean = 11.5 ± 2.9 mm, N = 4). The surface of the internal wall also had a coating of resin, and a deposit of debris. The resin became very hard after some time, and in some cases, mixed with the mud, made the wall even harder.

Females of *P. goryanum* hunted adult cockroaches of the genus *Eunyctibora* sp. (Epilampridae, Nyctiborinae) to provision their nests. In each nest, one (N = 1), two (N = 16), three (N = 5) or four (N = 1) prey were found (Fig. 1B). The egg, about 2 mm long, was laid behind the forecoxa of the prey (Fig. 1A, arrow). We observed that the locality where the egg was laid and the presence of adhering substances did not permit the prey to remove it. The prey remained paralyzed for only a short time, and in nests opened 2 days after closing we observed the cockroaches to be active and capable of flight. In nests controlled under laboratory conditions, eggs were only found in the very first prey brought into the nest; however, the cockroaches captured may have changed position. Female wasps preferred traps with 12.7 mm aperture (N = 103), although a few used those of 9.5 mm aperture (N = 11). The females did not build nests in traps of 4.8 mm aperture.

Development and life cycle

Time from egg to adult ranged between 38 and 48 days in 19 individuals, and in 6 other individuals between 81 and 198 days.

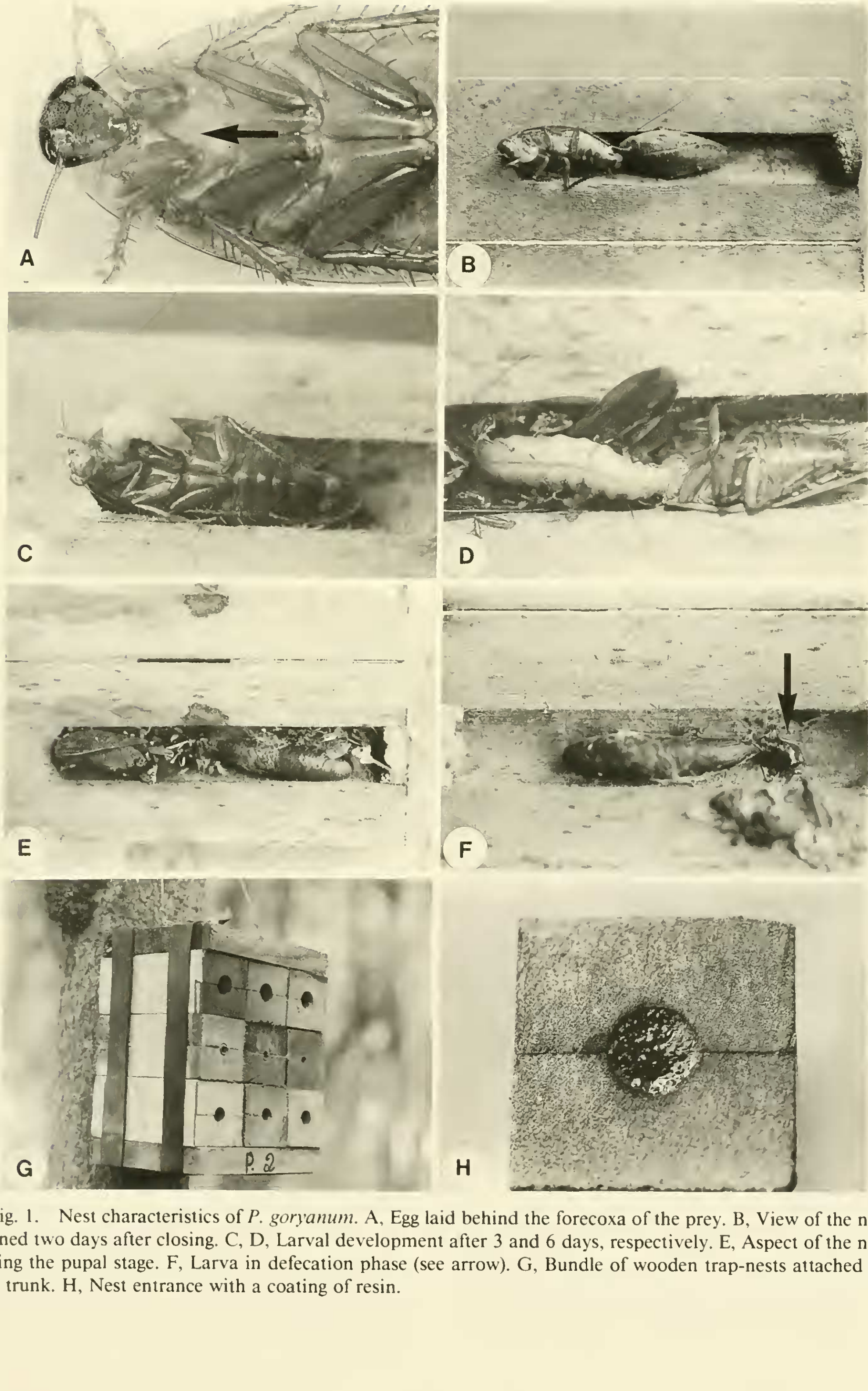

Fig. 1. Nest characteristics of *P. goryanum*. A, Egg laid behind the forecoxa of the prey. B, View of the nest opened two days after closing. C, D, Larval development after 3 and 6 days, respectively. E, Aspect of the nest during the pupal stage. F, Larva in defecation phase (see arrow). G, Bundle of wooden trap-nests attached on tree trunk. H, Nest entrance with a coating of resin.

In the second case, dormancy was observed in the prepupal stage.

The larva hatched after two days and remained behind the forecoxa of the prey where it began to feed by introducing part of the head and the body (Fig. 1C). The feeding period lasted 6 to 8 days (mean = 7.2 ± 0.6, N = 8), at the end of which the larva attained 2–3 cm in length. All of the internal contents of the prey was consumed, even the smaller parts such as the femur and head were emptied (Fig. 1D).

Between the end of the feeding period and the construction of the cocoon, the larva remained practically immobile for about 24 hours. Cocoon construction took about 48 h. It began with the production of fine silken threads that were attached at various points along the tunnel walls. The larva first constructed a silk mesh around the body, maintaining it suspended, and then began the construction of the cocoon wall. Initially the cocoon was transparent and eventually became dark amber (with a brittle cocoon wall after drying), and ranged between 27–37 mm in length (mean = 30.0 ± 3.6, N = 15) (Fig. 1E). At the posterior end of the cocoon an orifice remained opened through which feces were eliminated. The feces hardened after they dried, obstructing the opening and, in some cases, fixing the cocoon to the wall (Fig. 1F, arrow). The prepupal stage lasted 9–12 days (mean = 10.0 ± 1.2, N = 4), or 48–176 days (mean = 127.4 ± 46.5, N = 8) for individuals which entered dormancy. The pupal stage lasted 20–27 days (mean = 23.6 ± 2.4, N = 12). In all individuals reared in the laboratory, males were produced in greater numbers than females (28 ♂♂ : 10 ♀♀).

Nesting activity

The greatest nesting activity occurred between December and March (rainy season, but forest not flooded) and June through September (dry season, forest flooded). The maximum of provisioned cells occurred in February and August (Fig. 2: bottom). The correlation of nesting frequency with precipitation and the water level was not significant (r = 0.22, N = 12, $P = 0.49$ and r = 0.41, N = 12, $P = 0.18$, respectively) (see Fig. 2: top). The chi-square test indicated no significant difference in the nesting frequency among the types of wood ($\chi^2 = 4$, df = 4, $P = 0.41$) (Table 1).

Mortality and parasites

In 53% of the nests examined the individuals did not reach the adult stage. Among the causes of mortality, 80% unknown, we observed parasitism by *Melittobia* sp. (Eulophidae, Hymenoptera) (15%), *Anthrax* sp. (1.6%) and *Lepidophora* sp. (1.6%) (Bombyliidae, Diptera), and an unidentified species of Perilampidae, Hymenoptera (1.6%).

Discussion

Fricke (1992) observed that the nesting frequency of *Passaloecus* spp. (Pemphredoninae, Sphecidae) varied according to the tree species in which trap-nest bundles were attached, and suggested that the availability of natural nesting cavities, closure material such as resin, and the presence of suitable prey nearby were the reasons for this selection of nesting sites. Although we do not know the tree species where *P. goryanum* nests naturally, the random selection for nesting in traps made of various woods shows that the type of wood chosen for the traps did not influence nesting rates (Table 1).

Bohart and Menke (1976) placed members of *Penepodium* in three species groups, *goryanum, luteipenne* and *foeniforme.* As described by Williams (1928), *P. luteipenne* and *P. haematogastrum* (*luteipenne* group) excavate their nests in the ground or in banks. Richards (1937) cited *P. mocsaryi* (*goryanum* group) as collecting mud, and gave a record of a female of *P. goryanum* collected at the moment that it was inserting a cockroach into an abandoned tunnel of a *Passalus* sp. (Coleoptera) in a rotten stump. Williams also observed *P. goryanum* gathering mud.

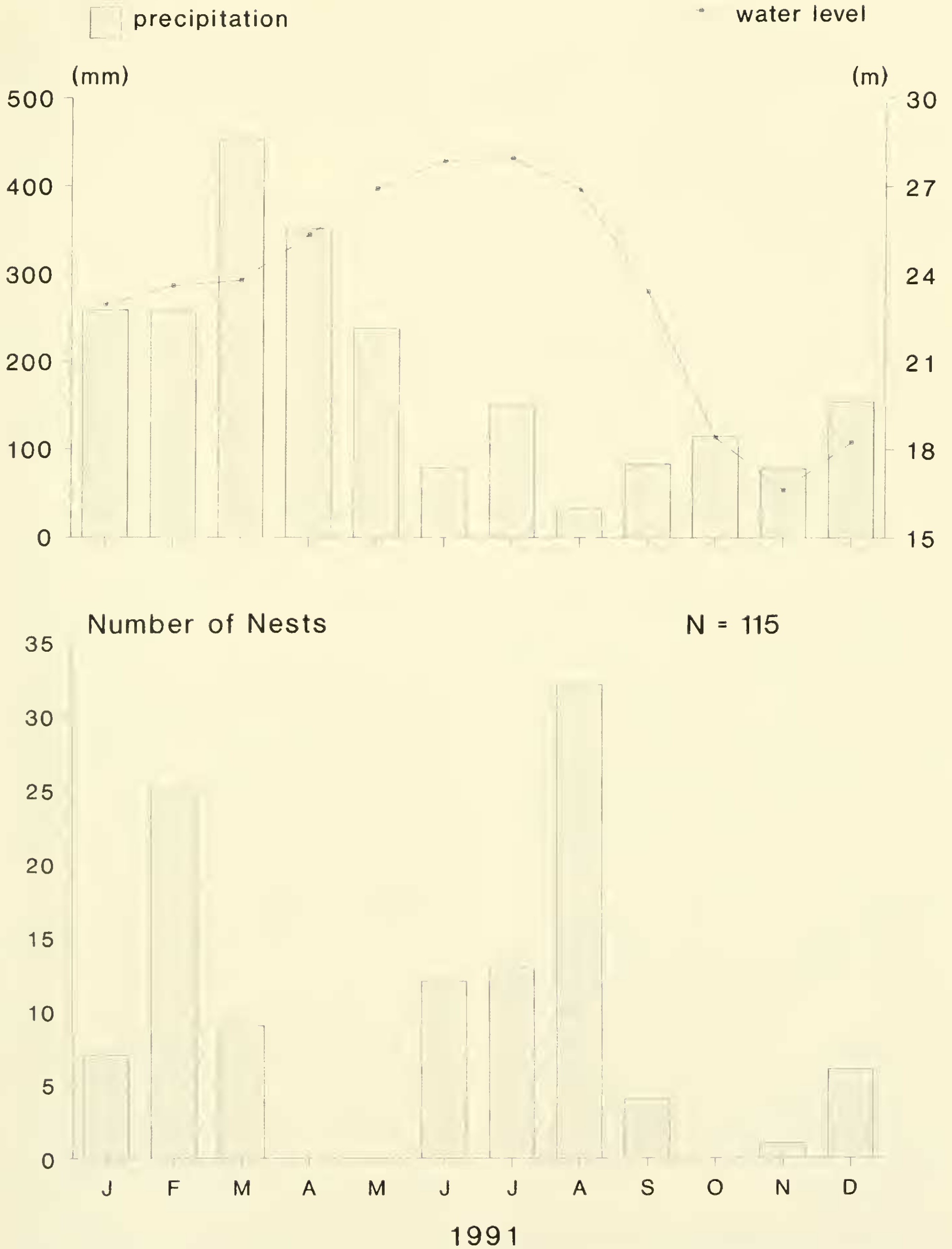

Fig. 2. Top, Annual precipitation and water level. Bottom, Nesting activity of *P. goryanum.*

Table 1. Nesting frequency of *P. goryanum* for different wood species.

Species	Trap-nests Frequency (9.5 and 12.7 mm)	Observed Frequency	Expected Frequency*	(χ^2)
Aldina latifolia	4	2	3.2	(0.45)
Mora paraensis	4	3	3.2	(0.0125)
Macrolobium acaciaefolium	4	1	3.2	(1.5125)
Triplaris surinamensis	4	5	3.2	(1.0125)
Protium sp.	4	5	3.2	(1.0125)

* $\chi^2_{\mathrm{Total}} = 4$, df = 4, $P = 0.41$.

Various behavioral characteristics have been used for diagnosis of species, genera or families of solitary wasps (cf. Evans 1966). Based on William's and Richard's observations, Bohart and Menke (1976) suggested, that the *luteipenne* species group excavates nests in the ground, and that the *goryanum* species group nests in pre-existing cavities. Our observations confirm that *P. goryanum* uses pre-existing cavities.

In sphecid wasps the preference for prey may occur at the subfamily, generic or species level; thus, the type of prey can be a useful taxonomical tool. The species of *Penepodium* studied by Williams (1928) provisioned their nests with cockroaches of the genus *Epilampra* Burmeister. We observed *P. goryanum* collecting cockroaches of the genus *Eunyctibora* Shelford; the specimens appeared to be conspecific.

According to Coville (1982), in the United States, wasps of the subgenus *Trypargilum* spp. are usually univoltine and overwinter in diapause in the prepupal phase, and in tropical regions they are bivoltine or "multivoltine" (= plurivoltine). Probably, in tropical climates the availability of prey is the principal factor responsible for the development of reproductive strategies in sphecid wasps.

The great variation in developmental times between individuals of *P. goryanum*, because of dormancy in the prepupal stage, probably is a strategy used to overcome adverse conditions such as humidity or scarcity of prey. Various studies have shown that in tropical forests some insect groups can have their seasonality and abundance triggered by food availability, and that even small changes in rain pattern can have a great effect on the quantity and availability of food (Wolda 1978). Fisk (1982) verified a seasonal variation in a population of cockroaches in the forest canopy in Panama and Costa Rica. They were abundant during the rainy season, coinciding with the greatest leaf production, and scarce during the dry season when there were fewer leaves. Fisk also observed that some genera, *Epilampra* among them, did not occur in the canopy, and probably were more abundant on the ground. Irmler and Furch (1979), studying populations of *Epilampra irmleri* Rocha e Silva and Aguiar in our same study site, observed that it was abundant in the litter during low water, reaching 75% of the total cockroach population.

Although we do not have observations on the ecology of *Eunyctibora*, it is possible that the nesting activity of *P. goryanum* is linked to the population fluctuations of the prey, probably caused by the flood pulse (cf. Junk et al. 1989). If the prey (*Eunyctibora* sp.) has terricolous habits, it is probable that at the beginning and at the end of the inundation it becomes scarce because of low reproductive rates when the individuals are migrating from the ground to the canopy and canopy to ground. On the other hand, if it is an arboricolous species, it is affected by predation or competition by the terricolous migrating fauna, particularly in March and April, the beginning of the forest inundation, and at the end of it, in September (cf. Adis 1992b). The variation in abundance of *P. goryanum* during the year can only be called seasonality if the pattern repeats itself in different years and our data as yet does not permit us to know whether this is the case.

ACKNOWLEDGMENTS

We would like to thank Dr. Sérvio Túlio P. Amarante (Museu de Zoologia, University of São Paulo, Brazil) and Dr. Arnold Menke (USDA, U.S. National Museum, Washington, D.C., USA) for identification of the wasps, and Dr. Cláudio José Becker (Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil) for identifying the cockroaches. Dr. Karl V. Krombein (Smithsonian Institution, Washington, D.C.) and Dr. Arnold Menke are thanked for valuable comments on the manuscript.

LITERATURE CITED

Adis, J. 1992a. How to survive six months in a flooded soil: Strategies in Chilopoda and Symphyla from Central Amazonian floodplains. Symposium on life-history traits in tropical invertebrates. INTECOL, Yokohama, Japan 1990. (J. Adis and S. Tanaka, eds.). Studies on Neotropical Fauna and Environment 27(2-3): 117–129.

———. 1992b. Überlebensstrategien terrestrischer Invertebraten in Überschwemmungswäldern Zentralamazoniens. Verhandlungen des naturwissenschaftlichen Vereins in Hamburg. (NF)33: 21–114.

Bohart, R. M. and A. S. Menke. 1976. Sphecid Wasps of the World. University of California Press, Berkeley. 695 pp.

Collins, J. A. and D. T. Jennings. 1984. A simplified holder for eumenid nesting blocks (Hymenoptera: Eumenidae). Entomological News 95(2): 58–62.

Coville, R. E. 1982. Wasps of the genus *Trypoxylon* subgenus *Trypargilum* in North America (Hymenoptera: Sphecidae). University of California Publications in Entomology 97: 1–147.

Coville, R. E. and P. L. Coville. 1980. Nesting biology and male behavior of *Trypoxylon* (*Trypargilum*) *tenoctitlan* in Costa Rica (Hymenoptera: Sphecidae). Annals of the Entomological Society of America 73: 110–119.

Evans, H. E. 1966. The behavior patterns of solitary wasps. Annual Review of Entomology 11: 123–154.

Fisk, F. W. 1982. Abundance and diversity of arboreal Blattaria in moist tropical forests of the Panama canal area and Costa Rica. Transactions of the American Entomological Society 108(4): 479–489.

Fricke, J. M. 1991. Trap-nest design for small trap-nesting Hymenoptera. The Great Lakes Entomologist 24(2): 121–122.

———. 1992. Influence of tree species on frequency of trap-nest use by *Passaloecus* species (Hymenoptera: Sphecidae). The Great Lakes Entomologist 25(1): 51–53.

Irmler, U. and K. Furch. 1979. Production, energy, and nutrient turnover of the cockroach *Epilampra irmleri* Rocha e Silva and Aguiar in a Central-Amazonian inundation forest. Amazoniana 6(4): 497–520.

Jayasingh, D. B. and B. E. Freeman. 1980. The comparative population dynamics of eight solitary bees and wasp (Aculeata: Apocrita: Hymenoptera) trap-nested in Jamaica. Biotropica 12(3): 214–219.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems. *In* Dodge, P., ed., Proceedings of the International Large River Symposium. Canadian Special Publication of Fisheries and Aquatic Sciences 106: 110–127.

Krombein, K. V. 1967. Trap-nesting Wasps and Bees: Life Histories, Nests and Associates. Smithsonian Press, Washington, D.C. 570 pp.

Matthews, R. W. and R. L. Fischer. 1964. A modified trap-nest for twig-nesting Aculeata. Proceedings. North Central Branch. Entomological Society of America 19: 79–81.

Medler, J. T. 1967. Biology of *Trypoxylon* in trap nests in Wisconsin (Hymenoptera: Sphecidae). American Midland Naturalist 78: 344–358.

Medler, J. T. and R. E. Fye. 1956. Biology of *Ancistrocerus antilope* (Panzer) (Hymenoptera, Vespidae) in trap-nests in Wisconsin. Annals of the Entomological Society of America 49: 97–102.

Ribeiro, M. de N. G. and J. Adis. 1984. Local rainfall variability—a potential bias for bioecological studies in the Central Amazon. Acta Amazônica 14: 159–174.

Richards, O. W. 1937. Results of the Oxford University expedition to British Guiana, 1929. Hymenoptera, Sphecidae and Bembecidae. Transactions of the Royal Entomological Society of London 86: 101–118.

Williams, F. X. 1928. Studies in tropical wasps—Their hosts and associates (with descriptions of new species). Bulletin of the Experiment Station of the Hawaiian Sugar Planters' Association, Entomological Series 19: 1–179.

Wolda, H. 1978. Seasonal fluctuations in rainfall, food and abundance of tropical insects. The Journal of Animal Ecology 47: 369–381.